Marine Ecology Progress Series
April 2016, Volume 547 Pages 193-209
http://dx.doi.org/10.3354/meps11641
http://archimer.ifremer.fr/doc/00334/44501/

Potential use of marinas as nursery grounds by rocky fishes: insights from four *Diplodus* species in the Mediterranean

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Abstract :

The construction of marinas along the shoreline has caused substantial habitat destruction within the sheltered coastal areas previously used as nursery grounds by many fish species. However, although the negative ecological impacts of these constructions have been reported extensively, their potential roles in the functioning of the coastal zone remain largely unknown. Here, we surveyed the juveniles of 4 *Diplodus* species in 5 marinas located along the French Mediterranean coast to assess whether rocky fishes can successfully settle inside these artificialized coastal areas. Inter-specific differences in the spatiotemporal use of the various artificial habitats provided by marinas were investigated between April and August over 2 consecutive years. We also tested the potential benefit of pegging additional artificial habitats (Biohuts) on docks and pontoons to increase their value as fish nursery grounds. Our results suggest that although variations in marina and artificial habitat preferences exist between species, *Diplodus* juveniles repeatedly colonize marinas. Their average abundances on added Biohut habitats were twice as high as on nearby bare surfaces. This suggests that increasing the complexity of the vertical structures of marinas can considerably enhance their suitability for juvenile rocky fishes, especially at the youngest stages, when mortality is highest. Therefore, as long as marina water quality is well controlled, ecological engineering within these man-made habitats might reduce the ecological consequences of urban development by providing suitable alternative artificial nursery grounds for rocky fishes.

Keywords : Coastal areas, Habitat anthropization, Fish juveniles, Sparids, Habitat preferences, Ecological engineering, Biohut

1. Introduction

Until recently, most research in urban ecology has focused on terrestrial habitats (e.g., Clergeau et al. 2006, Hobbs et al. 2006). However, more than three billion people currently live within 200 km of the sea, and this number is predicted to double by 2025 (Creel 2003). As a result, the destruction of coastal habitats is one of the main threats to marine ecosystems (Lotze et al. 2006, Airoldi & Beck 2007, Seaman 2007, Halpern et al. 2008), through its combined effects on biodiversity and ecosystem functioning (Beck et al. 2001, Courrat et al. 2009, Verdiell-Cubedo et al. 2013, Seitz et al. 2014, Sundblad et al. 2014). Although many different types of man-made structures dominate the shoreline, ecological issues relating to the introduction of infrastructures in shallow coastal waters have received little attention so far (Chapman & Blockley 2009, Bulleri & Chapman 2010) and we are just beginning to understand their impact on marine organisms, especially fishes (Duffy-Anderson et al. 2003).

Marinas are among the most common man-made infrastructures found on the shoreline. Their construction not only leads to the direct destruction of natural shallow water habitats, but also causes indirect damage through changes to currents and sediment loads that both have a dramatic impact on the composition of benthic communities (Meinesz et al. 1991, Martin et al. 2005) and fish larval dispersal and recruitment (Roberts 1997). Moreover, the industrial and yachting activities associated with marinas result in chronic biological and chemical pollutions of both the sediment and the water column inside and in the vicinity of marinas, which can have long-term consequences on living organisms (Bech 2002, Falandysz et al. 2002, Neira et al. 2011). All these factors lead to modifications of the ecological functions of the zones where marinas are built (Airoldi et al. 2005). However, the new shallow water habitats created within marinas might support new ecological functions.

The identification of nursery habitats is particularly important for stock conservation because mortality rates in fish are maximal during the early phases of their life cycles (Macpherson et al. 1997, Jennings & Blanchard 2004). Until now, very few studies have investigated the fish populations associated with marina structures. However, the peripheral breakwaters of marinas are often colonized by marine rocky fishes, at both the juvenile (Ruitton et al. 2000, Pizzolon et al. 2008, Dufour et al. 2009, Pastor et al. 2013) and adult stages (Guidetti 2004, Clynick 2006, Pizzolon et al. 2008, Cenci et al. 2011). Fish species richness on these artificial structures is generally equivalent to that of natural zones, and fish abundances are sometimes higher (Perez-Ruzafa et al. 2006). The number of fish species and the abundances of the most common rocky species inside marinas also seem to be similar to those found in natural habitats (Clynick et al 2008). As a result, shallow and protected habitats on the inshore sides of marina breakwaters could provide suitable nursery grounds for some of these fish species (Dufour et al. 2009). In theory, fish nursery grounds are defined according to four parameters: they support high abundances of juveniles, sustain faster somatic growth rates, allow higher survival and their populations contribute more to the final adult stock (Beck et al. 2001). At first sight, featureless and steep sloping marina structures, provided for example by docks and floating pontoons, seem unlikely to meet these definition criteria. Nevertheless, high abundances of juvenile rocky fishes have been observed on these artificial structures (Clynick 2008). Although not a definitive test, many authors (e.g., Cheminee et al. 2013, Pastor et al. 2013) have used the abundance criterion alone to identify nursery grounds among juvenile habitats. In this context, we decided to investigate the condition for the potential use of marina vertical structures as nursery grounds by rocky fish species, by surveying small-scale spatiotemporal changes in juvenile abundances for four sparids of the same genus (*Diplodus*, Raffinesque 1810) within five contrasting marinas located along the French Mediterranean coast (North-West Mediterranean). The main aims of this study were: (1) to see whether certain infra-littoral rocky fishes could successfully settle on the artificial vertical structures commonly found inside the marinas, and (2) to investigate how the juveniles of different species make use of the artificial habitats available. However, we also wanted to (3) test the potential benefit of ecological engineering within marinas to increase their value as rocky fish nursery grounds. Indeed, increasing the complexity of vertical structures has been shown to augment biodiversity in artificial aquatic habitats (Browne & Chapman 2014). For rocky fishes, this could also enhance juvenile survival by providing shelter against predators (Bulleri & Chapman 2010). Therefore, increasing the complexity of vertical structures inside marinas could enhance their value as fish nursery grounds, with potentially important consequences in terms of population dynamics.

2. Materials and methods

2.1. Species studied

This study focused on the juveniles of four species of the *Diplodus* genus: the annular seabream *D. annularis* (Linnaeus, 1758), the sharp snout seabream *D. puntazzo* (Cetti, 1777), the white seabream *D. sargus sargus* (Linnaeus, 1758), hereafter *D. sargus*, and the two-banded seabream *D. vulgaris* (Geoffroy Saint-Hilaire, 1817). These species are common in the Mediterranean and have high ecological and commercial value (Coll et al. 2004, Morales-Nin et al. 2005, Lloret et al. 2008). They are highly abundant in both natural and artificial rocky coastal areas (Tortonese 1965) and their juveniles are present in high abundances inside marinas, at least along the internal side of peripheral breakwaters (Clynick 2006). Natural settlement patterns are fairly well described for all four species: *D. annularis*, *D. puntazzo* and *D. sargus* all settle in one pulse, in June-July, October-November and May-June respectively, while *D. vulgaris* settles in two pulses, in November-December and in January-February, the first pulse being the more predominant (García-Rubies & Macpherson 1995, Harmelin-Vivien et al. 1995, Vigliola et al. 1998, Cheminee et al. 2011, Ventura et al. 2014). In *Diplodus* species, physical habitat characteristics (substrate, depth, level of protection from the prevailing winds, etc.) strongly determine both settlement success and pre-recruitment mortality (Harmelin-Vivien et al. 1995, MacPherson 1998, Vigliola & Harmelin-Vivien 2001, Cheminee et al. 2011, Ventura et al. 2014). *Diplodus puntazzo* and *D. sargus* both usually settle in very shallow parts (< 1 m) of small crannies characterized by gentle slopes covered with pebbles or sand. *Diplodus vulgaris* seems to prefer deeper waters (1-6 m) and can settle on a wider range of substrates (coarse sand, gravel, pebbles or boulders). Finally, settlement in *Diplodus annularis* occurs at even greater depths (> 5 m) but almost exclusively on seagrass beds (Harmelin-Vivien et al. 1995, Ventura et al. 2014). The species is thought to remain sedentary on the same seagrass bed for the entire duration of its juvenile life, while in *D. puntazzo, D. vulgaris* and *D. sargus*, substrate specificity disappears progressively during juvenile life, resulting in horizontal then vertical migrations (MacPherson 1998, Vigliola & Harmelin-Vivien 2001, Ventura et al. 2014). Given the differences in settlement dates and natural habitat preferences between these four species, the investigation of the variation in their respective abundances and habitat preferences between different types of marina should allow reaching global conclusions on the conditions of use of these man-made habitats by juvenile rocky fishes.

2.2. Study area

One hundred and fifty five marinas are listed along the French Mediterranean coast (Pinar Genc & Guler 2012). Our study was carried out within five of them, located at distances ranging from 20 to 180 km along the coasts of the Gulf of Lions and the French Riviera, in the towns of Port-Vendres, Port-Barcarès, Cap d'Adge, Mèze and Le Brusc (Fig. 1). These five marinas have all been in operation for over forty years and each harbors more than 200 pleasure craft; however, they have different surface areas, depths and surrounding environmental characteristics (Table 1). Port-Vendres marina is the deepest (8 m on average). Surrounded by a rocky coast, it covers a surface of 33 ha. The Cap d'Agde marina was also built on a rocky peninsula but it can harbor up to 3 100 boats (on 53 ha), so it is the most artificialized of the five. Le Brusc marina is the smallest (8 ha), but also the closest to natural conditions. It was constructed on a rocky shore, near one of the last four *P. oceanica* barrier reefs remaining in the French Mediterranean (Boudouresque et al. 1985). With a surface area of 81 ha, Port-Barcarès marina is very shallow (2 m on average). It was constructed in the channel connecting the Salses-Leucate lagoon to the sea and therefore communicates easily with the two habitats. The Mèze marina is also linked to a lagoon (Thau) but has no direct link with the sea (although it ultimately communicates with it through the three exits of the lagoon). Because these five marinas all have very different topographies and levels of human impact, the study of their respective use by fish juveniles should allow generalizing our results.

2.3. Surveys

Juvenile fish abundances and sizes were monitored along with water temperature (T in °C) in all five marinas, every two weeks for five consecutive months (April - August) in 2013 and in 2014. Due to logistic constraints, this timespan could not be extended to include the settlement dates for *D. puntazzo* (October-November) and *D. vulgaris* (November-December) (Harmelin-Vivien et al. 1995, Vigliola et al. 1998). However, it corresponds to the main period when the juveniles of all four species are found in natural coastal areas (Harmelin-Vivien et al. 1995, MacPherson 1998, Vigliola et al. 1998). Therefore we expected it to also cover most of the period for their joint presence in the marinas. Two different artificial vertical structures frequently found in marinas were compared in our work: vertical docks and floating pontoons. For each of them, two types of conditions were investigated: the structure (i.e. docks or pontoons) left bare (for control) or equipped by patented multifaceted devices specially designed to increase substrate complexity and facilitate fish post-larval settlement in man-made coastal habitats ("Biohut®"). The latter were consistently positioned under the surface of the water on both structures and immersed at least one month before the start of the annual surveys to harmonize benthic fauna densities between Biohut and controls. For each marina, three distinct zones containing only docks and three distinct zones containing pontoons were used as replicates. They were consistently separated by at least 20 m and positioned to encompass most of the local variability in physico-chemical conditions.

The sizes and locations of the surface areas of docks and pontoons dedicated respectively to Biohut positioning and to control surveys in each zone were chosen to harmonize Biohut surfaces between artificial structures and based on the minimum dimensions of the docks and the pontoons across all marinas. As a result, the Dock Biohut (DB) consisted of eight pegged cages measuring 0.5 × 0.8 × 0.25 m grouped along a 5 m long dock section and covering a total vertical surface of 4 m². Each DB cage was composed by two inseparable parts: an empty part and a part filled with oyster shells to maximize the surface for benthic fauna development (Fig. 2.a and 2.c). The Pontoon Biohut (PB) consisted of three cages measuring 0.5 × 0.8 × 0.34 m suspended under the pontoons by polyurethane ropes to provide a total vertical surface of ca. 4m². Each PB cage was composed of three inseparable parts: one part filled with oyster shells surrounded by two empty ones (Fig.2 b and 2d). Each replicate dock zone contained one DB and one control, the later consisting in a 5 × 0.8 m (4 m^2) vertical surface of bare dock (hereafter DC for Dock Control). Similarly, each replicate pontoon zone contained one PB and one control, the later consisting in a vertical surface of 4 m^2 positioned on the upper part of a pile used to anchor the pontoon (hereafter PC for Pontoon Control). In all replicate zones (dock or pontoon), the distance between the Biohut and the control was always of at least 10 m.

For each replicate dock and pontoon zone, a submersible data logger (IbCod 22L) was positioned to record water temperature (T in °C) hourly during the five months of the study (April -August) and surveys of juvenile fish abundances and sizes were scheduled every two weeks on all four artificial habitat types (AH, referring to DB, DC, PB and PC).

Abundances for all species were estimated by underwater visual census using stationary point counts, as they are particularly appropriate in restricted areas with homogeneous habitats (Bohnsack & Bannerot 1986, Clynick 2008, La Mesa et al. 2011). To do this, individual fish were always counted for three minutes. The surveys were carried out between 10:00 am and 4:00 pm and poor visibility and evident chemical or bacterial pollution conditions were consistently avoided. For each replicate zone, the survey of the docks was designed to include four successive stationary point counts per AH (one per pair of cages for DB and one per m^2 of bare dock surface for DC), so both DB and DC were each surveyed for 12 minutes. Moreover, for each replicate zone, the survey of the pontoons consisted of three successive point counts per AH (one point count per cage for PB and one per 1.33 m^2 of pile for PC), so their survey took nine minutes each. As a result, fish counts took 24 minutes in a dock zone, 18 minutes in a pontoon zone, and underwater visual censuses of 126 minutes were needed for the complete survey of each marina.

During the visual censuses, the juveniles of the four species were discriminated according to the morphological and size criteria given in Fishbase.com (Froese & Pauly 2014). All the juveniles identified were counted and their sizes (total length, TL) were estimated to the nearest 5 mm. To minimize bias in this estimation, fish silhouettes of different sizes were printed on plastic slates and used *in situ* by the divers (García-Rubies & Macpherson 1995, Harmelin-Vivien et al. 1995). When *in* *situ* identification was difficult, pictures and videos of individuals were taken and interpreted once back at the laboratory, with the assistance of expert Underwater Visual Census (UVC) divers. The same two divers worked throughout the sampling period.

In order to investigate changes in habitat use within the marinas, the juveniles of all species were also classified *a posteriori* into three successive development stages, according to the size ranges provided by Vigliola & Harmelin-Vivien (2001) for *D. sargus*, *D. vulgaris* and *D. puntazzo*, and by Ventura et al. (2014) for *D. annularis* (Table S1). Irrespective of the species, the "post-settlement" stage refers to the smallest individuals found during the short time-period that immediately follows benthic settlement (Vigliola & Harmelin-Vivien 2001). The "intermediate" stage is longer and includes juveniles of medium sizes that usually colonize all suitable habitats within the nursery ground. Finally, the "pre-dispersal" stage refers to the largest individuals that have acquired adult-like morphology and are ready to leave the nursery ground.

2.5. Statistical analysis

All calculations and statistical analyses were performed using the PRIMER 6 software with the PERMANOVA add-on (Clarke & Warwick 2001) or using the R software (R Core Team 2014) and indicspecies package. The significance level for the tests was consistently set at $\alpha = 0.05$.

Preliminary data analyses showed that the sampling year had no significant effect on juvenile *Diplodus* abundances and produced negative variance component estimates in all models but one (that for *D. sargus*). Therefore, following Fletcher & Underwood (2002), the data for the two consecutive years sampled in this work were consistently analyzed pooled, to reduce the effect of random variability in fish abundances among fish counts for certain AH and species, and thereby give a more robust image of the overall patterns of marina use by juvenile rocky fishes.

As the corresponding data were not normally distributed, spatial differences in water temperatures during the period studied (April-August) were investigated using a non-parametric Kruskal-Wallis test followed by Steel-Dwass-Critchlow-Fligner bilateral pairwise tests. Spatio-temporal variations in fish abundances (in numbers of individuals per count, hereafter ind. count^{-1}) were analyzed for all four species, separately or grouped, according to the month, the marina and the AH. For this, we performed three-way univariate PERMANOVAs since this method allows the handling of complex, unbalanced and multiple-factors designs, considers interaction among factors and does not assume a normal distribution of errors (Anderson 2001). Fish abundances were log(X+1) transformed prior to the generation of Euclidean distance similarity matrixes, and the factors 'Month' (with five levels: April to August) and 'AH' (with four levels: DB, DC, PB and PC) were treated as fixed, while the 'Marina' factor (with five levels: Port-Vendres, Port-Barcarès, Cap d'Adge, Mèze and Le Brusc) was treated as random. In addition to the main PERMANOVA test, contrasts were used to compare fish abundances between DB and DC and between PB and PC (Glasby 1997). P-values were calculated by 9999 random permutations of residuals under a reduced model and Type III sum of square (Anderson 2001).

For each species, ontogenetic changes in habitat use during juvenile life in marinas were also investigated, by identifying the type(s) of AH(s) preferred at each development stage using the Indicator Value index (IndVal) (Dufrêne & Legendre 1997). This composite index was originally developed to compare populations between sites and link species to communities based on habitat conditions (De Cáceres & Legendre 2009). It combines two estimates of habitat use for each species: specificity (S) and fidelity (F), based respectively on the species' relative abundance and its relative frequency of occurrence among sites or habitat types. Therefore it gives precise and accurate information on species habitat preferences (Legendre & Legendre 1998). In the present study, we applied it to explore differences in AH preferences within the marinas between all the development stages of the four species. Therefore development stages (post-settlement, intermediate and pre-dispersal) by species were used instead of species in IndVal calculations per AH, following the formula:

$$\mathrm{IndVal}_{ijk} = 100 \times S_{ijk} \times F_{ijk}$$

with specificity S_{ijk} defined by:

S_{ijk} = Abundance$_{ijk}$/Abundance$_{ij.}$

where Abundance$_{ijk}$ is the mean abundance per count of the development stage i of the species j in the AH k and Abundance$_{ij.}$ is the sum of the mean abundances per count of the same stage i of the same species j over all AH.

and with fidelity F_{jk} defined by:

$F_{jk} = N_{ijk}/N_{..k}$

where N_{ijk} is the number of the survey with at least one individual of the development stage i of the species j in the AH k, and $N_{..k}$ is the total number of surveys for this AH during the all study.

In order to generalize our results, IndVal was also calculated per development stage for all four species grouped. Differences in IndVal values between AH were tested by 9999 random permutations among groups (De Cáceres & Legendre 2009).

3. Results

Due to unexpected adverse environmental conditions in the marinas (e.g., occasional days with poor underwater visibility, pollution events) or logistic constraints on some of the sampling dates scheduled during the two years of the study, finally only 896 surveys were performed of the 1 200 initially planned. This did not however prevent accurate investigation of fish AH use in the five marinas, since all the sites were fully surveyed at least twice per month over the whole duration of the study when considering the two years pooled. However, pooling data from the two years can bias estimates of variance in some analyses and caution should be taken when interpreting the results. Similarly, logistic constraints in 2013 allowed performing only one stationary count per replicate zone for the controls, so the vertical surfaces investigated for DC and PC in this year covered only 4 m^2 per marina, instead of 12 m^2 in 2014. This should not however affect our conclusions since fish abundances on controls for 2014 were similar (PERMANOVA, $p > 0.5484$) when using one or all stationary counts, irrespective of the species or the marina.

Water temperatures in April-August differed significantly according to the survey site ($p < 0.0001$, Fig. S2), with higher and lower averages in Mèze (22.37 ± 3.77°C) and in Port-Vendres (19.39 ± 3.29°C), respectively, than in the three other marinas (19.76 ± 3.40°C in Port-Barcarès, 20.49.76 ± 3.16°C in Cap d'Agde and 20.56 ± 3.21°C in Le Brusc).

3.1. Juvenile fish abundances in the marinas

Over the time period surveyed, the maximum number of *Diplodus* juveniles observed throughout one point count was 60 individuals (on 15/04/2013 on a DB habitat in the Cap d'Agde marina). However, single counts with no observation were very frequent (83 %), and occurred irrespective of month or location. Finally, a total of 1 766 observations of *Diplodus* juveniles were made within the five marinas. However, most of the juveniles counted were *D. vulgaris* (N= 653) or *D. annularis* (N= 520), while observations were less frequent for *D. sargus* (N= 388) and *D. puntazzo* (N= 205). Spatiotemporal patterns of marina use varied greatly between species (Table 2, Fig. S1). Significant interactions between the 'Month' and 'Marina' factors in the PERMANOVAs for all four species, whether grouped or not (Table 2), also indicated that the temporal variations in juvenile abundances were not consistent across locations. Although this complicated data interpretation, some general temporal and spatial trends could still be discerned.

Temporal variations in juvenile abundances were significant only for *D. annularis* and *D. sargus* (Table 2), with the highest abundances for these species being reached in August (mean: 0.73 ± 0.14 ind. count^{-1}) and in July (mean: 0.48 ± 0.14 ind. count^{-1}), respectively. Temporal trends in the abundances of the post-settlement juveniles of the two species allowed identifying their respective periods of settlement in the marinas, in June-July for *D. sargus* and in July-August for *D. annularis* (Fig. 3). Similarly, a detailed analysis of the temporal variations in abundance for the post-settlement and pre-dispersal development stages of *D. puntazzo* and *D. vulgaris* suggested that settlement in the marinas probably occurred before the sampling period (April-August) for both these species, and suggested that their departure from the marinas started from July at certain locations (in particular Port-Vendres, Fig. 3). It is probable that sampling was stopped well before *D. annularis* dispersal because very few pre-dispersal individuals were observed for this species and most of its juveniles were still at the intermediate stage in August (Fig. 3).

Regarding general spatial trends, the number of observations of *Diplodus* juveniles varied considerably between marinas, with a total of 646 individuals being counted in Cap d'Agde, 393 in Le Brusc, 387 in Port-Vendres, 337 in Port-Barcarès, and only three in Mèze. Accordingly, juvenile abundance differed significantly between locations ($p < 0.001$, Table 2), with a maximum (1.08 ± 0.18 ind. count^{-1}) in Cap d'Agde and a minimum (0.04 ± 0.003 ind. count^{-1}) in the marinas of Mèze and Port-Barcarès, while similar intermediate values were obtained for Le Brusc and Port-Vendres (respectively of 0.85 ± 0.24, 0.96 ± 0.15 and 0.98 ± 0.14 ind. count^{-1}, respectively).

Species composition also depended on location, with spatial variations in juvenile abundance concerning all four species (Table 2), but differently (Fig. S1). Indeed, juveniles from all four species were observed in Port-Vendres, Port-Barcarès, Cap d'Agde and Le Brusc, while only three individuals of *D. vulgaris* were seen in Mèze (one post-settler in April and two pre-dispersal juveniles in June, observed on a DC and on a DB, respectively). Over the April-August period, the global average abundance of juveniles per count was maximum in Le Brusc for *D. annularis* (0.53 ± 0.14 ind. count^{-1}), in Port-Vendres for *D. puntazzo* (0.24 ± 0.05 ind. count^{-1}), in Port-Barcarès for *D. sargus* (0.67 ± 0.23 ind. count^{-1}) and in Cap d'Agde for *D. vulgaris* (0.55 ± 0.16 ind. count^{-1}). This may suggest differences in habitat suitability for *Diplodus* juveniles between the five marinas investigated, with further variation between the marinas according to species.

With regards effects of the artificial habitat type, abundances for the four species grouped were on average twice higher on the Biohut (mean: 1.02 ± 0.12 ind. count^{-1}) than on the nearby bare vertical surfaces used as controls (mean: 0.52 ± 0.12 ind. count$^{-1.}$). The significance of the interactions Ma × DB-v-DC ($p = 0.012$) and Ma × PB-v-DC ($p = 0.002$) suggested that *Diplodus* abundances were higher on Biohut than on controls irrespective of the artificial structure considered (dock or pontoon) but also revealed that this effect was strongly dependent on the location. Considering species separately revealed that, on the pontoons, this pattern concerned all four species (Ma × PB-v-PC, $p < 0.004$). On the docks however, the interaction was significant for *D. annularis* (Ma × DB-v-DC, $p = 0.001$), approached statistical significance for *D. vulgaris* ($p = 0.050$), but was not significant for *D. puntazzo* ($p = 0.364$) and *D. sargus* ($p = 0.807$). As a result, for docks, the month also had a significant effect on the global difference in *Diplodus* spp. abundances between Biohut on controls (Mo × DB-v-DC, $p = 0.004$).

3.2. Changes in habitat use during juvenile life

Our results revealed a generalized loss of habitat specificity during juvenile life in marinas in the four fish species investigated (Fig. 4). Indeed, when considering all *Diplodus* spp. grouped, IndVal values at the post-settlement stage were significantly higher ($p < 0.036$) for DB and PB than for DC and PC, reflecting a preference for Biohut habitats than for bare structures. At the intermediate stage, although IndVal values were still significantly higher ($p < 0.0001$) for DB and PB than for PC, the values for DB and DC were no longer statistically different ($p = 0.067$). Finally, at the pre-dispersal stage, IndVal did not differ significantly between any pair of habitat ($p > 0.057$), so no AH preference could be detected. This general trend was, however, slightly complicated by differences in AH preference between species, especially at the post-settlement and intermediate stages (Fig. 4). In *D. annularis*, IndVal values for DB and PB were similar ($p > 0.611$), irrespective of the development stage, and consistently higher ($p < 0.023$) than those of DC and PC. This indicated a preference for the Biohut habitats (on both docks and pontoons) in this species throughout its juvenile life within marinas. For the three other species investigated, ontogenetic shifts in habitat use were observed, all resulting in an absence of AH preference at the pre-dispersal stage ($p > 0.073$). *Diplodus vulgaris* settled essentially on DB, as indicated by the significantly higher ($p = 0.0001$) IndVal value found for this AH at the post-settlement stage. At the intermediate stage, it enlarged its habitat use to all dock habitats, which resulted in similar IndVal values for DB and DC ($p = 0.55$), both significantly higher ($p < 0.0003$) than those of PB and PC. In *D. puntazzo,* juveniles showed a preference for PB ($p < 0.032$) at the post-settlement stage, and then gathered preferentially around either of the two types of Biohut provided in the marinas. Thus, at the intermediate stage, the IndVal indexes for DB and PB in this species were significantly higher than those for DC and PC ($p < 0.014$) but did not differ significantly from each other ($p = 0.059$). Finally, post-settlement and intermediate juveniles of *D. sargus* had similar AH preferences. Their IndVal index for PB was significantly higher than that for DC ($p < 0.002$) but did not differ significantly from those of PC and DB ($p > 0.162$).

4. Discussion

To our knowledge, this is the first time that the use of man-made structures inside marinas, such as docks and pontoons found all around the world, by juvenile rocky fishes has been investigated this thoroughly. Juvenile fishes of the *Diplodus* genus were present on docks and pontoons in several of the marinas we investigated along the French Mediterranean coast. All four species were observed inside the marinas, and at all development stages (i.e. from post-settlement to pre-dispersal). However, even within these highly artificialized ecosystems, inter-specific variations in habitat preferences (mostly associated with the complexity of the vertical substrate available) were evidenced, especially at the youngest stages when mortality is highest (Macpherson et al. 1997). These findings have strong implications for the evaluation of the potential suitability of marinas as fish nursery grounds.

4.1. Conditions for the use of marinas as juvenile fish habitats

Juveniles of *Diplodus* spp. have already been reported in high numbers in the peripheral breakwaters of certain Mediterranean marinas (Ruitton 1999, Clynick 2006) but up to now no study has investigated their abundances on the AH present inside them. Our work shows that they are also present at all development stages on both the docks and the pontoons available inside the marinas. This suggests that docks and pontoons (or at least parts of them) have the potential to meet the habitat requirements for the successful settlement and juvenile growth of various *Diplodus* species in the Mediterranean.

This result was relatively unexpected, in particular for *D. annularis* for which juveniles were previously thought to be strongly associated with *P. oceanica* beds in the Mediterranean (Gordoa & Moli 1997, Garcia-Charton et al. 2004, Ventura et al. 2014). During the two summer months considered in this work, 520 juveniles of *D. annularis* were observed in the five marinas tested with high inter-location variability (Fig. S1). 54% and 42% of these observations were made on DB and PB, respectively. Since different protocols were used for the juvenile counts, the abundances measured in this study cannot be compared directly to those observed in natural areas. However, this result suggests that certain parts of marina ecosystems can allow the settlement of *D. annularis* juveniles. Pelagic fish larvae are known to often settle in the first suitable habitat they encounter (Shapiro 1987). Therefore, high abundances of *D. annularis* juveniles in certain marinas could partially result from an absence of suitable natural habitat in their immediate vicinity. This could be the case in Port-Barcarès, since this marina is located on a sandy coast, far from any *P. oceanica* bed. However, this explanation is not valid for the two marinas where the species was the most abundant (Le Brusc and Cap d'Agde), since they are both located in the neighborhood of one of the largest meadows of *P. oceanica* remaining along the Mediterranean coast (Boudouresque et al. 1985, Descamp et al. 2011). Therefore, our results suggest that plasticity in juvenile habitat requirements is probably higher than previously thought in *D. annularis*, and is maybe close to that already pointed out in the three other *Diplodus* species investigated (Guidetti 2004, Martin et al. 2005, Clynick 2006, Pastor et al. 2013). Further research should be conducted to investigate this possibility since an active selection of man-made artificial habitats by *Diplodus* larvae cannot be excluded, given the low levels of waving and the high trophic productivity often found in marinas (Planes et al. 1999, Dufour et al. 2009). Marinas could also act as light traps for the larvae at night (Doherty 1987). Whatever the case, plasticity in juvenile habitat requirements apparently allows successful settlement and growth of the juvenile fishes of this genus within certain marinas, despite the unavoidable pollution (by noise and by chemicals) associated with these man-made ecosystems (CETMEF 2010). If so, marinas could provide alternative nursery grounds for rocky fishes, at least in highly urbanized areas of the shoreline.

The presence and abundance of *Diplodus* juveniles varied greatly however according to the marina investigated. With only three juveniles (of *D. vulgaris*) observed during the whole period of our study, the marina of Mèze was barely colonized by the juveniles of this genus in 2013-14. The environmental conditions in this marina were apparently particular, since monthly temperatures during the study period were consistently at least 1°C higher in Mèze than in the four other sites investigated (Fig. S2). For many fish species, juvenile abundances strongly depend on water temperature, especially at the post-larval stage (e.g., Henderson & Seaby 1994, Félix-Hackradt et al. 2013). However, the juveniles of at least *D. vulgaris*, *D. annularis* and *D. puntazzo* usually settle successfully in environments with large differences in water temperature (18-29°C), salinities (18-39) and dissolved oxygen levels (2.7-9.6 mg. l^{-1}) (Vinagre et al. 2010). Therefore, it is quite unlikely that the main reason for the absence of *Diplodus* juveniles in Mèze lies in its environmental conditions. Another explanation could lie in the fact that this marina is located within the Thau lagoon, which the post-larvae must cross before reaching the marina. Indeed, in the nearby lagoon of Salses-Leucate, in which the salinity and temperature conditions are very close to those observed in Thau (Ifremer 2012), a marked reduction in the abundance of *D. sargus* juveniles has been noted over recent decades (Pastor et al. 2013). This phenomenon was attributed either to the increasing collection of *D. sargus* larvae by the artificial constructions built at the entrance of the lagoon, or to an augmentation of local juvenile mortality rates due to the degradation of environmental conditions in it. All the channels connecting the Thau lagoon to the sea are artificial and the Mèze marina is located at ca. 4 km from the nearest marine entrance. Therefore, the hypotheses proposed to explain the decline of juvenile *D. sargus* in Salses-Leucate (Pastor et al. 2013) could also apply in Thau and explain the lack of juveniles of the *Diplodus* genus in the Mèze marina, which has no direct connection with the sea where the breeding of the four species occurs (Harmelin-Vivien et al. 1995).

Juvenile fish abundances also varied between the four other marinas investigated, with almost twice as many individuals counted in Cap d'Agde as in Le Brusc, Port-Vendres and Port-Barcarès. Several hypotheses can be proposed to explain these spatial differences. For example, as the main direction of local currents and the presence of gyres can influence the dispersion or retention of fish eggs and larvae (Cheminee et al. 2011), pelagic larval inputs for each species may differ between marinas, depending on the location of their nearest spawning grounds. Some marinas might also be close to natural nursery areas and indirectly benefit from their attractiveness for the larvae. Another explanation might lie in the differences in mean depth between our marinas as this factor governs *Diplodus* spp. settlement in natural areas (Harmelin-Vivien et al. 1995). However, *Diplodus* abundances in our study showed no significant relation with marina depth. For example, the maximum abundances of *D. puntazzo*, a species known to naturally settle in very shallow coastal habitats (Harmelin-Vivien et al. 1995), were observed in the deepest marina (Port-Vendres). Finally, post-settlement mortality rates can differ between locations depending on both the physico-chemical conditions and local inter-specific competition for available resources (Planes et al. 1998). Apparently, of all the sites we studied, the vast (53 ha) and shallow (< 3 m) marina of Cap d'Agde is the most favorable for the settlement and growth of *Diplodus* juveniles, despite the fact that, with 58.5 rings. ha^{-1} on average, it has the highest density of use after the marina of Le Brusc (99.5 rings. ha^{-1}). This might be due to its location on a primarily rocky shore, or to the fact that it is surrounded by several *P. oceanica* meadows (Descamp et al. 2011). However, species composition also depended highly on location and maximum juvenile abundances were found in Cap d'Agde for *D. vulgaris* only. For the three other species, these abundances occurred in other marinas: in Le Brusc for *D. annularis*, in Port-Vendres for *D. puntazzo* and in Port-Barcarès for *D. sargus*. Therefore the factors responsible for spatial differences in juvenile abundances are probably multiple and depend on the species. They require investigation to better understand the potential value of marinas as nursery grounds for rocky fishes. However, our results clearly indicate that marinas do not all succeed in providing environmental conditions favorable for the settlement and survival of *Diplodus* juveniles. Thus the location and environmental characteristics of marinas should be considered first when trying to restore the potential nursery function of the littoral ecosystems in which they were built.

4.2 Ecological engineering: a tool for improving the nursery potential of marinas

Each marina consists in a mosaic of different artificial habitats, each characterized by specific biotic and abiotic features and supporting functionally different life stages or species. Our results showed that increasing their diversity can have a significant impact on the value of marinas as fish nursery grounds. Indeed, post-settlement stage juveniles were essentially found around the added Biohut structures, irrespective of whether they were installed on docks or on pontoons. But this result strongly depends on the marina considered as, due to their location or physico-chemical conditions they provide, some of them do not seem to meet environmental conditions for the successful *Diplodus* juveniles settlement. Such marinas (for example Mèze) probably cannot function as *Diplodus* nursery grounds and adding Biohut on docks or pontoons do not provide any ecological benefit.

In a natural context, early mortality of *Diplodus* juveniles is driven both by density-dependent processes linked to post-settlement intensity (Doherty 1981, 1991), and by density-independent processes linked to predation and refuge availability (Hixon 1991, Vigliola 1998). Although this has not yet been demonstrated, we can reasonably assume that these two types of processes also modulate the abundances of rocky fish juveniles in marinas. For example, differences in abundance between Biohut and controls in our study could be due to a reduction of juvenile mortality on Biohut, since they provide more refuge against predators than the featureless vertical surfaces usually found on docks and pontoons (Ammann 2004, Bulleri & Chapman 2010). In this case, the reason why habitat preference for Biohut in marinas was particularly observable for the youngest stages may lie in the fact that mortality by predation is highest at this period of life (Macpherson et al. 1997). Another explanation could lie in the attraction offered by complex solid structures (in our case the Biohut) for pelagic larvae, a behavior known as thigmotaxis (Ammann 2004). The two hypotheses are not mutually exclusive and, even if the Biohut was originally designed to protect the youngest juveniles from mobile predators, knowing whether they act on fish production by reducing post-settlement mortality or on fish density by attracting fish larvae by thigmotaxis requires further investigation.

Interestingly, habitat preference at the post-settlement stage was the least marked in *D. sargus* for which no significant differences in IndVal were observed between DB, PB and PC. This could be due to the higher plasticity in this species' juvenile habitat requirements (Cheminee et al. 2011, Pastor et al. 2013) or to a limitation in the availability of its most favorable habitats (Harborne et al. 2011). Indeed, when pre-settlement *D. sargus* arrive in the marinas (in June-July), Biohut habitats are still largely occupied by the post-settlement juveniles of *D. puntazzo* and *D. vulgaris* (Fig. S1). This might partly explain why they also settle abundantly under the bare pontoons. Therefore, as in natural habitats, high occupation rates of the most optimal habitats could lead to competitive interactions between species within marinas and force the late-breeding ones to settle on sub-optimal habitats.

Although our results suggest that ecological engineering in some marinas could increase their value as nursery grounds for rocky fishes, this also implies the preservation or improvement of their water and sediment quality. Indeed, in order to satisfy the definition of nursery area, habitats have to contribute considerably to the adult stock (Beck et al. 2001). Juvenile fish can experience very stressful environmental conditions in marinas (e.g., boat traffic, extensive pollutant loads, dredging, etc.) linked to human activities (CETMEF 2010). Chemical contaminants in particular are known to adversely affect fish physiology, growth, health and behavior, especially at young stages (e.g., Laroche et al. 2002, Marchand et al. 2003, Rowe 2003, Kerambrun et al. 2012). As in other organisms, sub-lethal responses to contaminant exposure in fish commonly involve a decrease in feeding activity (Stephens et al. 2000, Saborido-Rey et al. 2007) and a modification in energy allocation, which is preferentially used to fight chemical stress rather than for body maintenance and growth (Rowe 2003). This can have marked negative effects on global individual fitness, as fish juveniles with slow growth rates and limited energy storage have lower survival rates and contribute less to the adult stock (Sogard 1997). Therefore heavily contaminated marinas probably cannot function as fish nursery grounds. Since between 337 and 646 *Diplodus* juveniles were observed at all development stages in all but one marina (Mèze) tested for two consecutive years, the pollution in these particular locations is probably below critical pollution thresholds. However, our results might overestimate the actual abundances of *Diplodus* juveniles in marinas since the techniques applied in this study (underwater visual census by snorkelers) excluded heavily polluted sites from our investigations. Therefore, the impact of contaminant exposure during juvenile life (high and punctual or limited yet repeated) on the final fitness of fishes will have to be explored before concluding on the real value of marinas as nursery grounds.

4.3. Consistency in seasonality and changes in habitat use between natural and artificial habitats

In the Mediterranean, juvenile presence on nursery grounds is known to occur from May-June to late September in *D. sargus*, from July to September in *D. annularis*, from October to May-June in *D. puntazzo* and from November-December to June-July in *D. vulgaris*. Therefore, given our period of survey within marinas (April to August), abundance peaks in juveniles linked to recruitment were expected for *D. annularis* and *D. sargus* only. Similarly, artificial habitat preferences were estimated solely from the individuals present within the marinas from April to August. As a result, they were reliably assessed only for the post-settlement juveniles of *D. annularis* and *D. sargus*, the intermediate juveniles of all four species and the pre-dispersal juveniles of *D. puntazzo*, *D. vulgaris* and *D. sargus*. For the other fish groups, preferred habitat estimates should be considered with caution since they were extrapolations based on a reduced number of observations.

Temporal abundance patterns for the post-settlement juveniles of *D. sargus* and *D. annularis* indicated that, during the two years studied, their juveniles mainly arrived in the marinas in June and in July-August, respectively. This timing is consistent with the information gathered so far on their respective settlement periods in the Western Mediterranean, which can both show temporal variation of ca. one month between sites and years (see Ventura et al. 2014 for review). For *D. puntazzo* and *D. vulgaris,* post-settlement juveniles were observed only at the beginning of the survey period (from April to June) and were consistently accompanied by older juveniles. This suggests that both species settled in the marinas well before the start of the surveys (in April). Thus local adaptations to marina artificial habitats in *Diplodus* spp. apparently do not involve a modification in recruitment dates. It should be noted, however, that the observation of 12 post-settlement juveniles of *D. puntazzo* in several of the marinas investigated in April was relatively unexpected since this species settles in November – December on its natural nurseries (Harmelin-Vivien et al. 1995, Vigliola et al. 1998). Although errors (± 3.5 mm) in the estimation of fish size by visual census cannot be excluded (MacPherson 1998), so part of these *D. puntazzo* individuals could be at the boundary between post-settler and intermediate juvenile classes, they were particularly small (< 30 mm TL). Therefore further research should be conducted to investigate the reasons for their presence in the marinas at this period.

In Mediterranean natural coastal areas, ontogenetic shifts in habitat use are well documented for *Diplodus* species (MacPherson 1998, Vigliola & Harmelin-Vivien 2001, Ventura et al. 2014). In general, morphologic modifications during fish growth in this genus are accompanied by habitat changes, resulting in horizontal then vertical migrations (MacPherson 1998, Vigliola & Harmelin-Vivien 2001). In *D. annularis* however, fidelity to *P. oceanica* meadows is usually strong throughout juvenile life, except for the larger individuals that can be found on other substrates such as sandy areas (Ventura et al. 2014). This high habitat fidelity was also observed in the marinas, where the species was almost exclusively found in Biohut habitats, irrespective of the juvenile stage. Indeed, during the two years of our survey, *D. annularis* juveniles were observed only twice on DC and only three times on PC, and at very low abundances in both cases. Behavior in the artificial context of marinas is thus close to natural behavior, the juveniles of the species being highly associated with the most sheltered habitat available. Similarly, changes in habitat preferences during juvenile life for *D. sargus, D. vulgaris* and *D. puntazzo* juveniles in marinas mirrored those described in natural areas (MacPherson 1998). With increasing body size juvenile fish are less vulnerable to predation (Houde & Hoyt 1987), so their need for shelter decreases. They also diversify their diet toward bigger and more mobile prey, and experience lower inter- or intra-specific competition for food (Ross 1986, MacPherson 1998), driving them to enlarge their territory. Accordingly, in the marinas investigated, the youngest juvenile stages of *D. sargus, D. vulgaris* and *D. puntazzo* were essentially associated with the most sheltered (PB and/or DB), whereas the oldest ones were found to occur evenly on all the types of AH investigated. This was not anticipated because the habitats available within the marinas and in natural environments differ dramatically and fish species generally adapt their behavior to the habitat (Koeck et al. 2013).

5. Conclusions

By studying the abundances of *Diplodus* spp. juveniles in five marinas located along the French Mediterranean coast, we observed that these man-made littoral ecosystems, designed without considering their potential value as fish habitats, can contain high numbers of juvenile rocky fish which apparently remain there from settlement to dispersal. This had already been observed for other artificial habitats found in the coastal zone, including the breakwaters commonly found at the entrance of marinas. Nevertheless, the docks and pontoons commonly found inside marinas unexpectedly also seem to be suitable for fish settlement and growth, especially if artificial multifaceted devices are added to increase their structural complexity. This has important ecological implications since the entire surface of marina ecosystems might participate in the maintenance of rocky fish stocks along anthropized shorelines. However, water and sediment are often polluted in marinas, and the physical damage caused by the replacement of natural substrates with built infrastructures is irreversible. Therefore, even if some ecological functions can be conserved within man-made habitats, some are definitively lost and it seems unrealistic to pursue the hope of restoring marinas to pristine conditions. Public policies should therefore manage and protect natural fish nursery grounds prior to considering the potential improvement of marina quality as such. Whatever the case, the rehabilitation of the nursery function of the zones where marinas have been built cannot rely only on ecological engineering. The immediate and long-term effects of fish exposure to the contaminants found in marinas should also be studied to adequately improve their water and sediment quality. Finally, connectivity between artificial and natural habitats must be evaluated in order to prioritize restoration of the marinas that receive the highest numbers of larvae and contribute most to coastal adult stocks.

Acknowledgements

This work was conducted within the framework of the Nappex Project funded by the 'Agence de l'Eau Rhône Mediterranée et Corse', the ‘Conseil Général de l’Herault’ and the Ecocean Society in the framework of a call for tenders launched by the Ministry of the Environment and Sustainable Development in 2011.

Bibliographical references

Airoldi L, Beck MW (2007) Loss, status and trends for coastal marine habitats of Europe. In: Gibson RN, Atkinson RJA, Gordon JDM (eds) Oceanography and Marine Biology, Vol 45, Vol 45. Crc Press-Taylor & Francis Group, Boca Raton, p 345-405

Ammann AJ (2004) SMURFs: standard monitoring units for the recruitment of temperate reef fishes. Journal of Experimental Marine Biology and Ecology 299:135-154

Anderson JM (2001) Permutation tests for univariate or multivariate analysis of variance and regression. Canadian Journal of Fisheries and Aquatic Sciences 58:626-639

Bech M (2002) Imposex and tributyltin contamination as a consequence of the establishment of a marina, and increasing yachting activities at Phuket Island, Thailand. Environmental Pollution 117:421-429

Beck MW, Heck KL, Able KW, Childers DL, Eggleston DB, Gillanders BM, Halpern B, Hays CG, Hoshino K, Minello TJ, Orth RJ, Sheridan PF, Weinstein MR (2001) The identification, conservation, and management of estuarine and marine nurseries for fish and invertebrates. Bioscience 51:633-641

Bohnsack J, Bannerot SP (1986) A stationary visual census technique for quantitatively assessing community structure of coral reef fishes, Vol Technical Report 41. NOAA

Boudouresque CF, Meinesz A, Lefevre JR (1985) Mapping the marine benthic communities in Corsica. The *Posidonia oceanica* reef of Saint-Florent. Annales de l'Institut Oceanographique 61:27-38

Browne MA, Chapman MG (2014) Mitigating against the loss of species by adding artificial intertidal pools to existing seawalls. Marine Ecology Progress Series 497:119-129

Bulleri F, Chapman MG (2010) The introduction of coastal infrastructure as a driver of change in marine environments. Journal of Applied Ecology 47:26-35

Cenci E, Pizzolon M, Chimento N, Mazzoldi C (2011) The influence of a new artificial structure on fish assemblages of adjacent hard substrata. Estuarine Coastal and Shelf Science 91:133-149

CETMEF L (2010) Bilan national du RÉPOM-Réseau national de surveillance de la qualité des eaux et des sédiments des ports maritimes. 90 p

Chapman MG, Blockley DJ (2009) Engineering novel habitats on urban infrastructure to increase intertidal biodiversity. Oecologia 161:625-635

Cheminee A, Francour P, Harmelin-Vivien M (2011) Assessment of Diplodus spp. (Sparidae) nursery grounds along the rocky shore of Marseilles (France, NW Mediterranean). Scientia Marina 75:181-188

Cheminee A, Sala E, Pastor J, Bodilis P, Thiriet P, Mangialajo L, Cottalorda J-M, Francour P (2013) Nursery value of Cystoseira forests for Mediterranean rocky reef fishes. Journal of Experimental Marine Biology and Ecology 442:70-79

Clarke KR, Warwick RM (2001) Change in marine communities: an approach to statistical analysis and interpretation. PRIMER-E Limited Plymouth, UK

Clergeau P, Croci S, Jokimäki J, Kaisanlahti-Jokimäki M-L, Dinetti M (2006) Avifauna homogenisation by urbanisation: Analysis at different European latitudes. Biological Conservation 127:336-344

Clynick BG (2006) Assemblages of fish associated with coastal marinas in north-western Italy. Journal of the Marine Biological Association of the United Kingdom 86:847-852

Clynick BG (2008) Characteristics of an urban fish assemblage: Distribution of fish associated with coastal marinas. Marine Environmental Research 65:18-33

Coll J, Linde M, García-Rubies A, Riera F, Grau AM (2004) Spear fishing in the Balearic Islands (west central Mediterranean): species affected and catch evolution during the period 1975–2001. Fisheries Research 70:97-111

Courrat A, Lobry J, Nicolas D, Laffargue P, Amara R, Lepage M, Girardin M, Le Pape O (2009) Anthropogenic disturbance on nursery function of estuarine areas for marine species. Estuarine Coastal and Shelf Science 81:179-190

Creel L (2003) Ripple effects: Population and coastal regions, Vol. Population Reference Bureau Washington, DC

De Cáceres M, Legendre P (2009) Associations between species and groups of sites: indices and statistical inference. Ecology 90:3566-3574

Descamp P, Holon F, Ballesta L, Guilbert A, Guillot M, Boissery P, Raimondino V, Deter J (2011) Fast and easy method for seagrass monitoring: Application of acoustic telemetry to precision mapping of Posidonia oceanica beds. Marine Pollution Bulletin 62:284-292

Doherty PJ (1987) Light-traps: selective but useful devices for quantifying the distributions and abundances of larval fishes. Bulletin of Marine Science 41:423-431

Doherty PP (1981) Coral reef fishes: recruitment-limited assemblages? The Reef and Man. Proceedings of the 4th International Coral Reef Symposium, Manila Philippines, 18-22 May 1981-pages: 2: 465-470. Marine Sciences Center, University of the Philippines

Doherty PP (1991) Spatial and temporal patterns in recruitment Ecology of coral reef fishes. Academic Press, p 261-293

Duffy-Anderson JT, Manderson JP, Able KW (2003) A characterization of juvenile fish assemblages around man-made structures in the New York New Jersey Harbor Estuary, USA. Bulletin of Marine Science 72:877-889

Dufour V, Cantou M, Lecomte F (2009) Identification of sea bass (Dicentrarchus labrax) nursery areas in the north-western Mediterranean Sea. Journal of the Marine Biological Association of the United Kingdom 89:1367-1374

Dufrêne M, Legendre P (1997) Species assemblage and indicator species: the need for a flexible asymetrical approach. Ecological Monographs 67:345-366

Falandysz J, Brzostowski A, Szpunar J, Rodriguez-Pereiro I (2002) Butyltins in sediments and three-spined stickleback (Gasterosteus aculleatus) from the marinas of the Gulf of Gdansk, Baltic Sea. Journal of Environmental Science and Health Part a-Toxic/Hazardous Substances & Environmental Engineering 37:353-363

Félix-Hackradt FC, Hackradt CW, Treviño-Otón J, Segovia-Viadero M, Pérez-Ruzafa A, García-Charton JA (2013) Environmental determinants on fish post-larval distribution in coastal areas of south-western Mediterranean Sea. Estuarine, Coastal and Shelf Science 129:59-72

Fletcher DJ, Underwood AJ (2002) How to cope with negative estimates of components of variance in ecological field studies. Journal of Experimental Marine Biology and Ecology 273:89-95

Froese R, Pauly D (2014) Fishbase. Available: www.fishbase.org

Garcia-Charton JA, Perez-Ruzafa A, Saanchez-Jerez P, Bayle-Sempere JT, Renones O, Moreno D (2004) Multi-scale spatial heterogeneity, habitat structure, and the effect of marine reserves on Western Mediterranean rocky reef fish assemblages. Marine Biology 144:161-182

García-Rubies A, Macpherson E (1995) Substrate use and temporal pattern of recruitment in juvenile fishes of the Mediterranean littoral. Marine Biology 124:35-42

Glasby T (1997) Analysing data from post-impact studies using asymmetrical analyses of variance: A case study of epibiota on marinas. Australian Journal of Ecology 22:448-459

Gordoa A, Moli B (1997) Age and growth of the sparids *Diplodus vulgaris*, *D. sargus* and *D. annularis* in adult populations and the differences in their juvenile growth patterns in the north-western Mediterranean Sea. Fisheries Research 33:123-129

Guidetti P (2004) Fish assemblages associated with coastal defence structures in south-western Italy (Mediterranean Sea). Journal of the Marine Biological Association of the United Kingdom 84:669-670

Halpern BS, Walbridge S, Selkoe KA, Kappel CV, Micheli F, D'Agrosa C, Bruno JF, Casey KS, Ebert C, Fox HE, Fujita R, Heinemann D, Lenihan HS, Madin EMP, Perry MT, Selig ER, Spalding M, Steneck R, Watson R (2008) A global map of human impact on marine ecosystems. Science 319:948-952

Harborne AR, Mumby PJ, Kennedy EV, Ferrari R (2011) Biotic and multi-scale abiotic controls of habitat quality: their effect on coral-reef fishes. Marine Ecology Progress Series 437:201-214

Harmelin-Vivien ML, Harmelin JG, Leboulleux V (1995) Microhabitat requirements for settlement of juvenile sparid fishes on Mediterranean rocky shores. Hydrobiologia 300-301:309-320

Henderson PA, Seaby RMH (1994) On the factors influencing juvenile flatfish abundance in the lower Severn Estuary, England. Netherlands Journal of Sea Research 32:321-330

Hixon MA (1991) Predation as a process structuring coral reef fish communities. In: Sale P (ed) The Ecology of Fishes on Coral Reefs. Academic press, p 475-508

Hobbs RJ, Arico S, Aronson J, Baron JS, Bridgewater P, Cramer VA, Epstein PR, Ewel JJ, Klink CA, Lugo AE, Norton D, Ojima D, Richardson DM, Sanderson EW, Valladares F, Vilà M, Zamora R, Zobel M (2006) Novel ecosystems: theoretical and management aspects of the new ecological world order. Global Ecology and Biogeography 15:1-7

Houde E, Hoyt R (1987) Fish early life dynamics and recruitment variability. American Fisheries Society Symosium Series 2:17-29

Ifremer (2012) Réseau de Suivi Lagunaire du Languedoc-Roussillon. Bilan des résultats 2011. . Report No. 12/2012

Jennings S, Blanchard JL (2004) Fish abundance with no fishing: predictions based on macroecological theory. Journal of Animal Ecology 73:632-642

Kerambrun E, Henry F, Courcot L, Gevaert F, Amara R (2012) Biological responses of caged juvenile sea bass (*Dicentrarchus labrax*) and turbot (*Scophtalmus maximus*) in a polluted harbour. Ecological Indicators 19:161-171

Koeck B, Alos J, Caro A, Neveu R, Crec'hriou R, Saragoni G, Lenfant P (2013) Contrasting fish behavior in artificial seascapes with implications for resources conservation. PLoS ONE 8

La Mesa G, Molinari A, Gambaccini S, Tunesi L (2011) Spatial pattern of coastal fish assemblages in different habitats in North-western Mediterranean. Marine Ecology 32:104-114

Laroche J, Quiniou L, Juhel G, Auffret M, Moraga D (2002) Genetic and physiological responses of flounder (*Platichthys flesus*) populations to chemical contamination in estuaries. Environmental Toxicology and Chemistry 21:2705-2712

Legendre P, Legendre L (1998) Numerical Ecology, Volume 24, Developments in Environmental Modelling, Vol. Elsevier Science

Lloret J, Zaragoza N, Caballero D, Font T, Casadevall M, Riera V (2008) Spearfishing pressure on fish communities in rocky coastal habitats in a Mediterranean marine protected area. Fisheries Research 94:84-91

Lotze HK, Lenihan HS, Bourque BJ, Bradbury RH, Cooke RG, Kay MC, Kidwell SM, Kirby MX, Peterson CH, Jackson JBC (2006) Depletion, degradation, and recovery potential of estuaries and coastal seas. Science 312:1806-1809

MacPherson E (1998) Ontogenetic shifts in habitat use and aggregation in juvenile sparid fishes. Journal of Experimental Marine Biology and Ecology 220:127-150

Macpherson E, Biagi F, Francour P, Garcia-Rubies A, Harmelin J, Harmelin-Vivien M, Jouvenel JY, Planes S, Vigliola L, Tunesi L (1997) Mortality of juvenile fishes of the genus Diplodus in protected and unprotected areas in the western Mediterranean Sea. Marine Ecology Progress Series 160:135-147

Marchand J, Tanguy A, Laroche J, Quiniou L, Moraga D (2003) Responses of European flounder *Platichthys flesus* populations to contamination in different estuaries along the Atlantic coast of France. Marine Ecology Progress series 260:273-284

Martin D, Bertasi F, Colangelo MA, de Vries M, Frost M, Hawkins SJ, Macpherson E, Moschella PS, Satta MP, Thompson RC, Ceccherelli VU (2005) Ecological impact of coastal defence structures on sediment and mobile fauna: Evaluating and forecasting consequences of unavoidable modifications of native habitats. Coastal Engineering 52:1027-1051

MEDAM (2015) www.medam.org (assessed 04 April 2015)

Meinesz A, Lefevre JR, Astier JM (1991) Impact of coastal development on the infralittoral zone along the southeastern Mediterranean shore of continental France. Marine Pollution Bulletin 23:343-347

Morales-Nin B, Moranta J, García C, Tugores MP, Grau AM, Riera F, Cerdà M (2005) The recreational fishery off Majorca Island (western Mediterranean): some implications for coastal resource management. ICES Journal of Marine Science: Journal du Conseil 62:727-739

Neira C, Mendoza G, Levin LA, Zirino A, Delgadillo-Hinojosa F, Porrachia M, Deheyn DD (2011) Macrobenthic community response to copper in Shelter Island Yacht Basin, San Diego Bay, California. Marine Pollution Bulletin 62:701-717

Pastor J, Koeck B, Astruch P, Lenfant P (2013) Coastal man-made habitats: Potential nurseries for an exploited fish species, *Diplodus sargus* (Linnaeus, 1758). Fisheries Research 148:74-80

Perez-Ruzafa A, Grarcia-Charton JA, Barcala E, Marcos C (2006) Changes in benthic fish assemblages as a consequence of coastal works in a coastal lagoon: The Mar Menor (Spain, Western Mediterranean). Marine Pollution Bulletin 53:107-120

Pinar Genc E, Guler N (2012) Assessment of marinas in the Mediterranean and the position of Turkey. PROMET-Traffic&Transportation 18:207-213

Pizzolon M, Cenci E, Mazzoldi C (2008) The onset of fish colonization in a coastal defence structure (Chioggia, Northern Adriatic Sea). Estuarine Coastal and Shelf Science 78:166-178

Planes S, Jouvenel JY, Lenfant P (1998) Density dependence in post-recruitment processes of juvenile sparids in the littoral of the Mediterranean Sea. Oikos 83:293-300

Planes S, Macpherson E, Biagi F, Garcia-Rubies A, Harmelin J, Harmelin-Vivien M, Jouvenel JY, Tunesi L, Vigliola L, Galzin R (1999) Spatio-temporal variability in growth of juvenile sparid fishes from the Mediterranean littoral zone. Journal of the Marine Biological Association of the United Kingdom 79:137-143

R Core Team (2014) R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria

Roberts CM (1997) Connectivity and management of Caribbean coral reefs. Science 278:1454-1457

Ross ST (1986) Resource Partitioning in Fish Assemblages: A Review of Field Studies. Copeia 1986:352-388

Rowe CL (2003) Growth responses of an estuarine fish exposed to mixed trace elements in sediments over a full life cycle. Ecotoxicology and Environmental Safety 54:229-239

Ruitton S (1999) Les communautés benthiques et nectobenthiques associées aux aménagements littoraux en Méditerranée nord-occidentale. Structure et fonctionnement., Université d'Aix-Marseille II

Ruitton S, Francour P, Boudouresque CF (2000) Relationships between algae, benthic herbivorous invertebrates and fishes in rocky sublittoral communities of a temperate sea (Mediterranean). Estuarine Coastal and Shelf Science 50:217-230

Saborido-Rey F, Dominguez-Petit R, Tomas J, Morales-Nin B, Alonso-Fernandez A (2007) Growth of juvenile turbot in response to food pellets contaminated by fuel oil from the tanker 'Prestige'. Marine Ecology Progress Series 345:271-279

Seaman W (2007) Artificial habitats and the restoration of degraded marine ecosystems and fisheries. Hydrobiologia 580:143-155

Seitz RD, Wennhage H, Bergström U, Lipcius RN, Ysebaert T (2014) Ecological value of coastal habitats for commercially and ecologically important species. ICES Journal of Marine Science: Journal du Conseil 71:648-665

Shapiro DY (1987) Inferring larval recruitment strategies from the distribution ecology of settled individuals of coral-reef fish. Bulletin of Marine Science 41:289-295

Sogard SM (1997) Size-selective mortality in the juvenile stage of teleost fishes: A review. Bulletin of Marine Science 60:1129-1157

Stephens SM, Frankling SC, Stagg RM, Brown JA (2000) Sub-lethal effects of exposure of juvenile turbot to oil produced water. Marine Pollution Bulletin 40:928-937

Sundblad G, Bergstrom U, Sandstrom A, Eklov P (2014) Nursery habitat availability limits adult stock sizes of predatory coastal fish. ICES Journal of Marine Science 71:672-680

Tortonese E (1965) Biologie comparée de trois espèces méditerranéennes de Diplodus (Pisces Sparidae). Rapport Commission International pour l’Exploration Scientifique de la Mer Méditérranée 189-192

Ventura D, Jona Lasinio G, Ardizzone G (2014) Temporal partitioning of microhabitat use among four juvenile fish species of the genus Diplodus (Pisces: Perciformes, Sparidae). Marine Ecology:1-20

Verdiell-Cubedo D, Oliva-Paterna FJ, Ruiz-Navarro A, Torralva M (2013) Assessing the nursery role for marine fish species in a hypersaline coastal lagoon (Mar Menor, Mediterranean Sea). Marine Biology Research 9:739-748

Vigliola L (1998) Contrôle et régulation du recrutement des Sparidae (Poissons, Téléostéens) en Méditerranée : importance des processus pré- et post-installation benthique. Université Aix-Marseille II

Vigliola L, Harmelin-Vivien M (2001) Post-settlement ontogeny in three Mediterranean reef fish species of the genus Diplodus. Bulletin of Marine Science 68:271-286

Vigliola L, Harmelin-Vivien ML, Biagi F, Galzin R, Garcia-Rubies A, Harmelin JG, Jouvenel JY, Le Direach-Boursier L, Macpherson E, Tunesi L (1998) Spatial and temporal patterns of settlement among sparid fishes of the genus Diplodus in the northwestern Mediterranean. Marine Ecology Progress Series 168:45-56

Vinagre C, Cabral HN, Costa MJ (2010) Relative importance of estuarine nurseries for species of the genus Diplodus (Sparidae) along the Portuguese coast. Estuarine Coastal and Shelf Science 86:197-202

Table 1: Characteristics of the five marinas studied in this work. PV = Port-Vendres, BA = Port-Barcarès, CA = Cap d'Agde, ME = Mèze, BR = Le Brusc (Sources MEDAM 2015).

Marina	**Construction date**	**Surface area (ha)**	**Number of rings**	**Average depth (m)**	**Connection(s)**	**Coast type**
PV	1853	33	253	8	Sea	Rocky
BA	1963	81	950	2	Sea and Salses-Leucate lagoon	Sandy
CA	1969	53	3 100	3	Sea	Rocky
ME	6th century	18	200	2	Thau lagoon	Sandy
BR	1960	8	796	4	Sea	Rocky

Table 2: Results of the univariate three-way PERMANOVAs performed to compare juvenile fish abundances (ind. count^{-1}) between months (April to August), marinas (Port-Vendres, Port-Barcarès, Cap d'Agde, Mèze and Le Brusc) and artificial habitat type (DB, DC, PB and PC). Contrasts were used to compare juvenile fish abundances between DB vs DC and PB vs PC. Significant p values (< 0.05) are indicated in bold. A star (*)in the 'Source' column to indicates the results of contrast tests.

Source	df	MS	Pseudo-F	P(perm)
***Diplodus* spp.**				
Month (Mo)	4	1.3285	1.8282	0.1718
Marina (Ma)	4	6.2927	23.643	**0.0001**
Artificial Habitat Type (AH)	3	3.4027	4.0546	**0.0309**
*DB-v-DC	1	2.6958	2.8197	0.1742
*PB-v-PC	1	7.3272	7.4131	0.0619
Mo x Ma	16	0.737	2.769	**0.0005**
Mo x AH	12	0.6153	1.7594	0.0881
*Mo x DB-v-DC	4	0.74754	6.2743	**0.0036**
*Mo x PB-v-PC	4	0.27934	0.88306	0.4933
Ma x AH	12	0.84719	3.183	**0.0004**
*Ma x DB-v-DC	4	0.96961	3.2608	**0.0117**
*Ma x PB-v-PC	4	0.99439	4.2266	**0.0022**
Mo x Ma x AH	48	0.3522	1.3233	0.0771
*Mo x Ma x DB-v-DC	16	0.11284	0.37948	0.9883
*Mo x Ma x PB-v-PC	16	0.31847	1.3536	0.1618
Residuals	796	0.26616		
Total	895			
D. annularis				
Month (Mo)	4	2.9147	5.4272	**0.0052**
Marina (Ma)	4	1.2478	20.884	**0.0001**
Artificial Habitat Type (AH)	3	1.0537	3.4146	0.0506
*DB-v-DC	1	1.5682	6.1272	0.0778
*PB-v-PC	1	1.5927	2.7135	0.1796
Mo x Ma	16	0.54779	9.1682	**0.0001**
Mo x AH	12	0.5233	3.3548	**0.0011**
*Mo x DB-v-DC	4	0.79985	5.4357	**0.0053**
*Mo x PB-v-PC	4	0.76441	3.4679	**0.0286**
Ma x AH	12	0.31205	5.2228	**0.0001**
*Ma x DB-v-DC	4	0.26008	4.7304	**0.0011**
*Ma x PB-v-PC	4	0.59113	9.1692	**0.0001**
Mo x Ma x AH	48	0.15884	2.6584	**0.0002**
*Mo x Ma x DB-v-DC	16	0.15041	2.7356	**0.001**
*Mo x Ma x PB-v-PC	16	0.22453	3.4827	**0.0004**
Residuals	796	5.9749E-2		
Total	895			

Source	df	MS	Pseudo-F	P(perm)
D. puntazzo				
Month (Mo)	4	0.11838	1.7037	0.185
Marina (Ma)	4	0.58042	17.379	**0.0001**
Artificial Habitat Type (AH)	3	0.40819	2.1155	0.1367
*DB-v-DC	1	0.13055	5.1787	0.0947
*PB-v-PC	1	0.80851	1.9883	0.2246
Mo x Ma	16	7.0293E-2	2.1048	**0.0084**
Mo x AH	12	5.5525E-2	2.0167	**0.0413**
*Mo x DB-v-DC	4	2.2988E-2	2.6866	0.0726
*Mo x PB-v-PC	4	0.12138	2.6845	0.0708
Ma x AH	12	0.19517	5.8438	**0.0001**
*Ma x DB-v-DC	4	2.5248E-2	1.0828	0.3637
*Ma x PB-v-PC	4	0.40952	9.4409	**0.0001**
Mo x Ma x AH	48	2.7359E-2	0.8192	0.7967
*Mo x Ma x DB-v-DC	16	8.0345E-3	0.34458	0.99
*Mo x Ma x PB-v-PC	16	4.5265E-2	1.0435	0.4057
Residuals	796	3.3397E-2		
Total	895			
D. sargus				
Month (Mo)	4	1.3037	4.225	**0.0156**
Marina (Ma)	4	0.7363	9.4466	**0.0001**
Artificial Habitat Type (AH)	3	0.69136	1.5925	0.2432
*DB-v-DC	1	6.022E-2	4.8709	0.0998
*PB-v-PC	1	0.29581	0.60032	0.4789
Mo x Ma	16	0.31376	4.0256	**0.0002**
Mo x AH	12	0.17219	1.1333	0.354
*Mo x DB-v-DC	4	1.056E-2	0.33165	0.8579
*Mo x PB-v-PC	4	0.14321	1.0896	0.3924
Ma x AH	12	0.4391	5.6336	**0.0001**
*Ma x DB-v-DC	4	1.2007E-2	0.40495	0.8068
*Ma x PB-v-PC	4	0.49567	3.9417	**0.0042**
Mo x Ma x AH	48	0.15413	1.9775	**0.0007**
*Mo x Ma x DB-v-DC	16	3.1919E-2	1.0765	0.3708
*Mo x Ma x PB-v-PC	16	0.13158	1.0463	0.4124
Residuals	796	7.7943E-2		
Total	895			

Source	df	MS	Pseudo-F	P(perm)
D. vulgaris				
Month (Mo)	4	0.56464	1.9424	0.1555
Marina (Ma)	4	1.4537	12.35	**0.0001**
Artificial Habitat Type (AH)	3	1.9162	3.709	0.0433
*DB-v-DC	1	1.5172E-3	3.0143E-3	0.9144
*PB-v-PC	1	1.3173E-3	0.0069712	0.9741
Mo x Ma	16	0.29459	2.5029	**0.0017**
Mo x AH	12	0.26063	1.4489	0.1845
*Mo x DB-v-DC	4	8.1717E-2	0.78894	0.5441
*Mo x PB-v-PC	4	6.4966E-2	1.2575	0.3328
Ma x AH	12	0.5222	4.4367	**0.0001**
*Ma x DB-v-DC	4	0.50927	2.3585	0.0509
*Ma x PB-v-PC	4	0.1903	9.3036	**0.0001**
Mo x Ma x AH	48	0.18172	1.5439	0.0149
*Mo x Ma x DB-v-DC	16	9.9605E-2	0.46128	0.9627
*Mo x Ma x PB-v-PC	16	5.2481E-2	2.5657	**0.0028**
Residuals	796	0.1177		
Total	895			

Fig. 1: Location of the five marinas studied along the French Mediterranean coast.

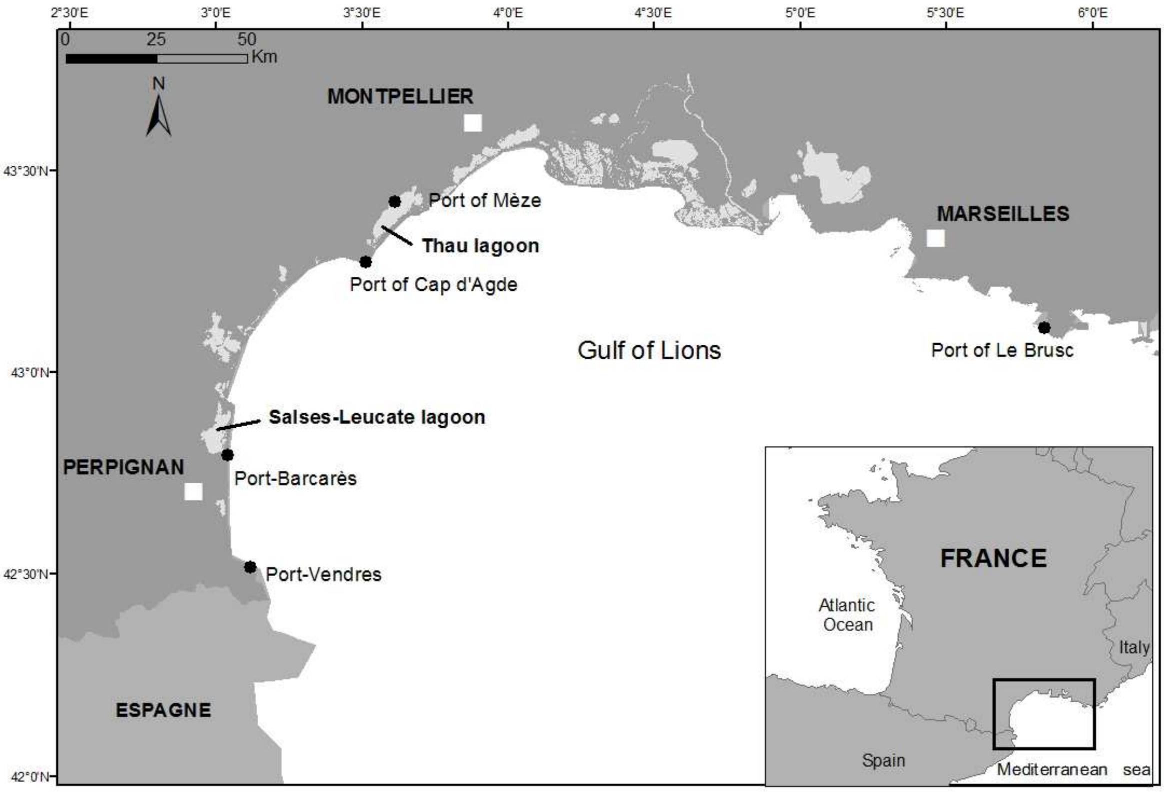


Fig 2. (a) Dock Biohut® steel cage including (1) a part filled with oyster shells (0.5 x 0.8 m, 2.5 cm mesh size) and (2) an empty part (0.5 x 0.8 m, 5 cm mesh size). (b) Pontoon Biohut® steel cage including (1) a part filled with oyster shells (0.5 x 0.8 m, 2.5 cm of mesh size) and (2) two empty parts (0.5 x 0.8 m, 5 cm of mesh size). (c) Dock Biohut sampling unit (DB) corresponding to eight adjacent cages pegged on 5m of dock, (d) Pontoon Biohut (PB) cage fixed under a floating pontoon with polyurethane ropes.

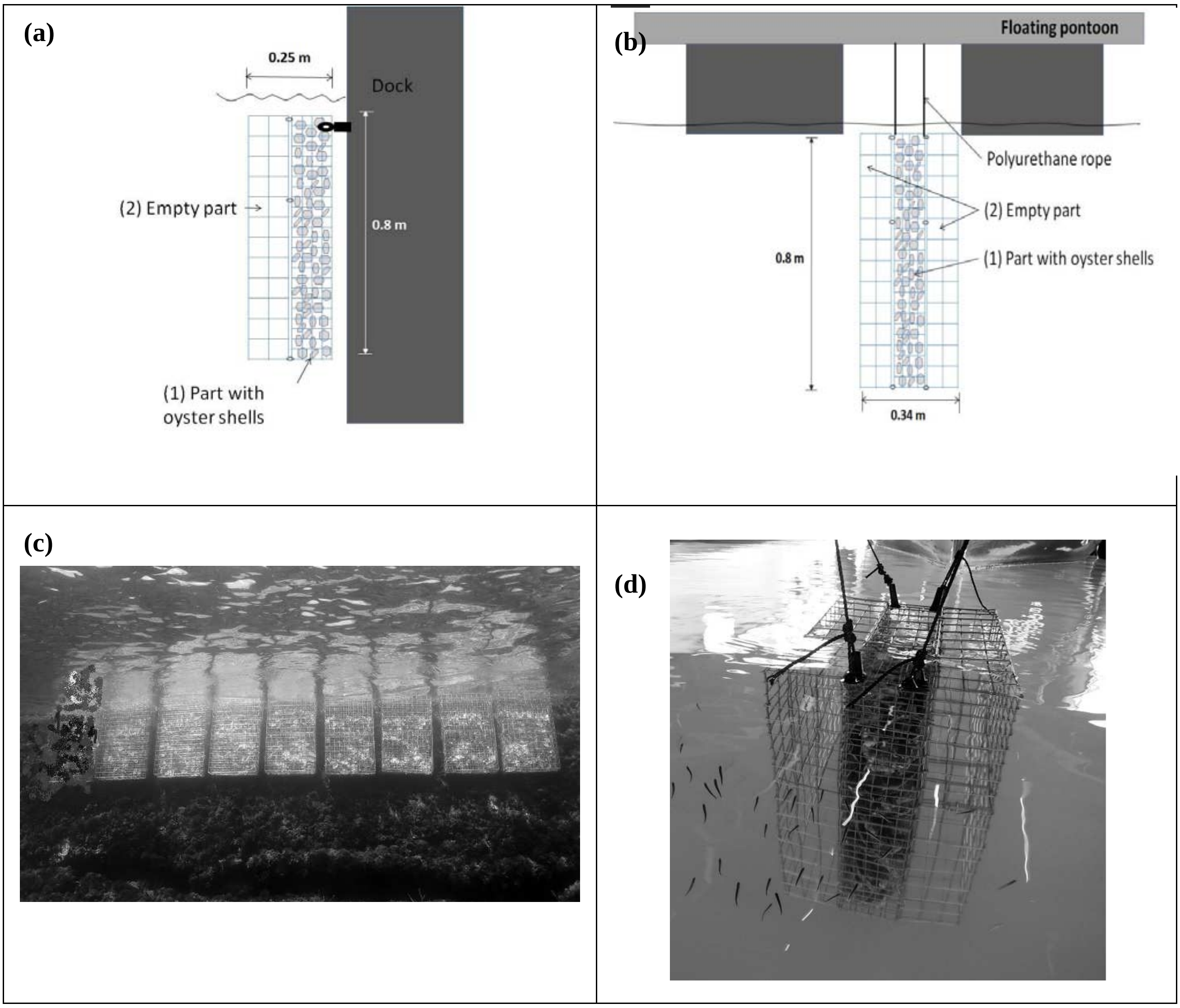


Fig. 3: Average monthly abundances of juveniles (expressed in ind. count^{-1}) at the post-settlement, intermediate and pre-dispersal stages observed for the four *Diplodus* species investigated. Results for all locations, artificial structures and artificial habitats are pooled. Error-bars represent standard errors around the means.

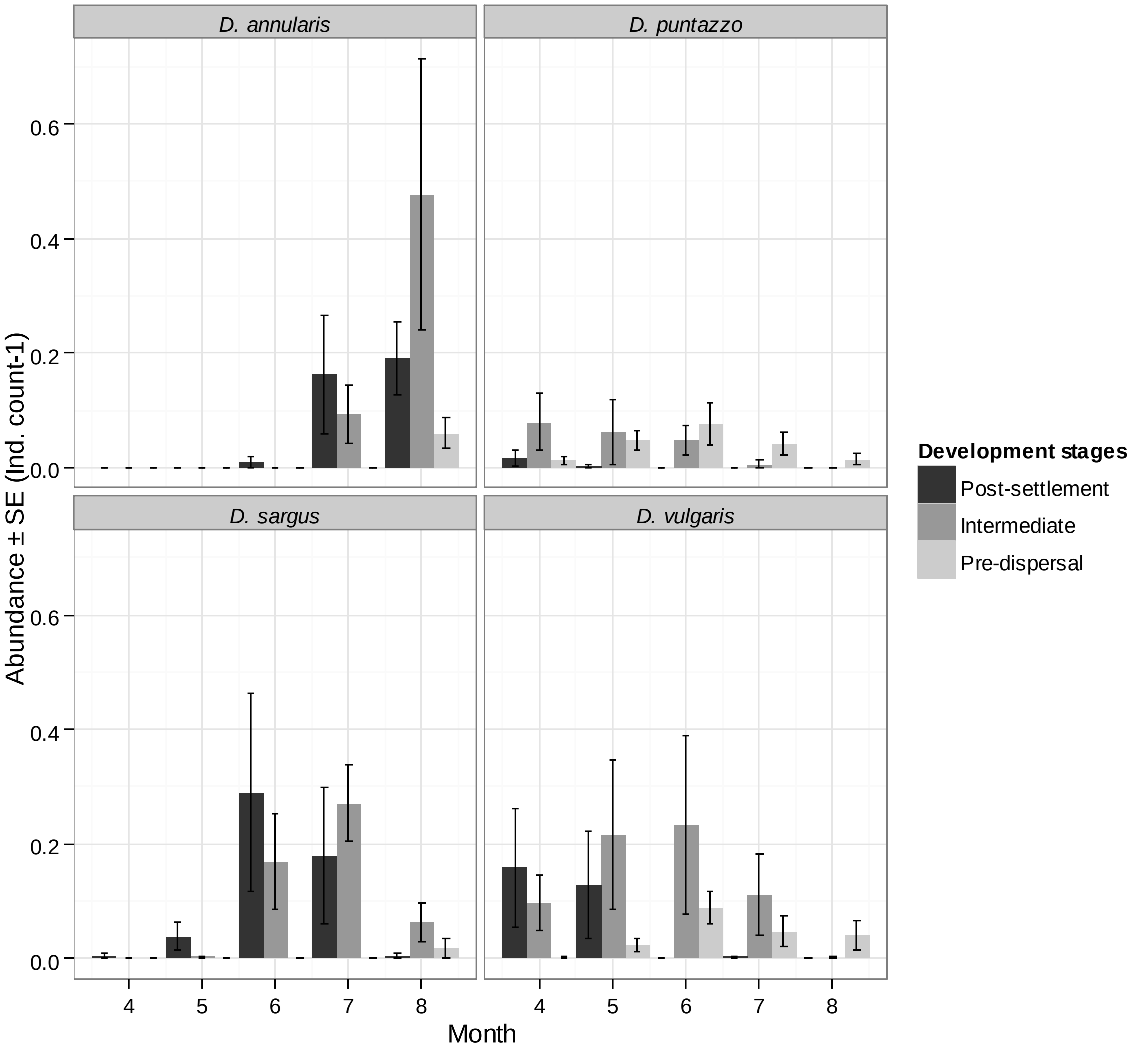
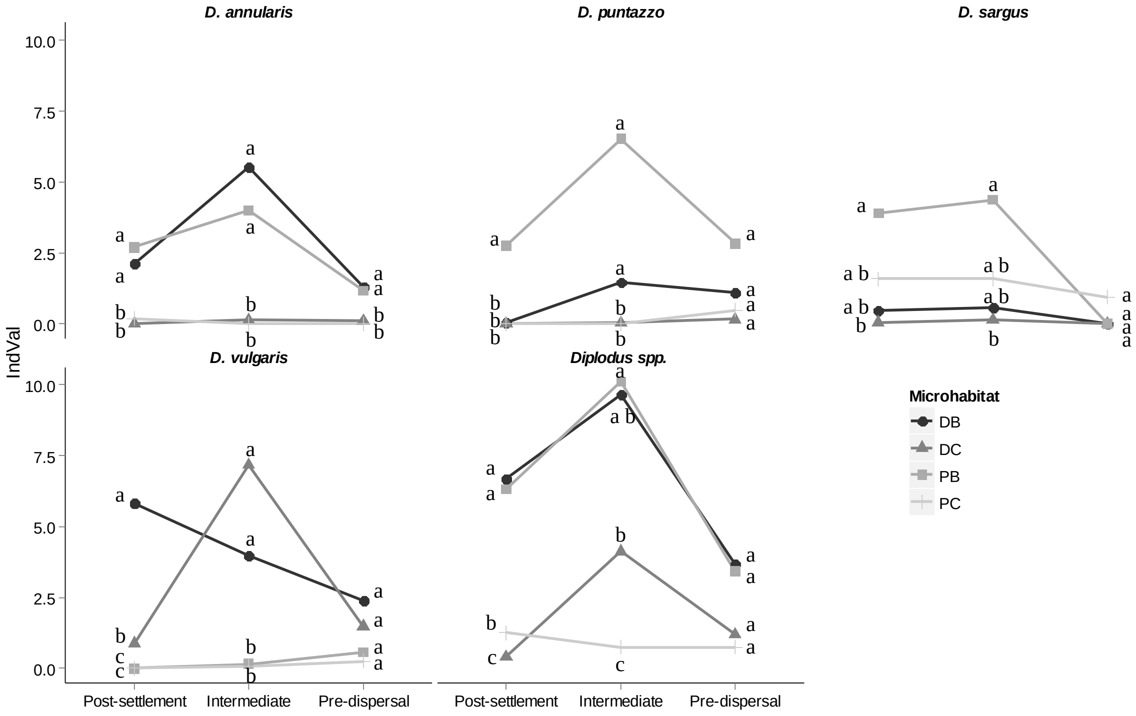
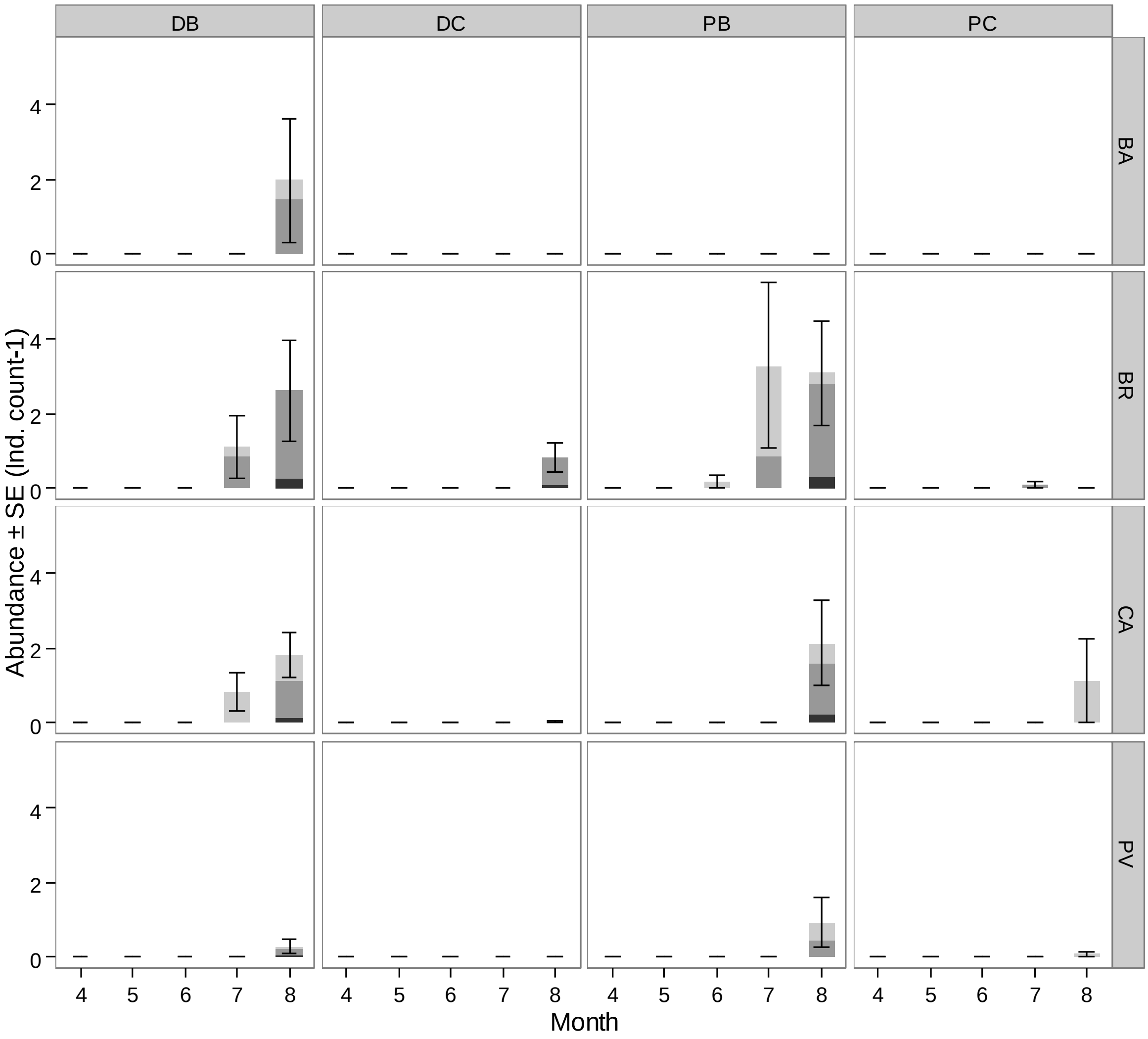


Fig. 4: Indicator Value indexes (Dufrêne & Legendre 1997) per habitat type obtained for all three development stages (post-settlement, intermediate and pre-dispersal) in the four *Diplodus* species considered grouped or separately. For each development stage, artificial habitats presenting differences in their IndVal indexes are given different letters.

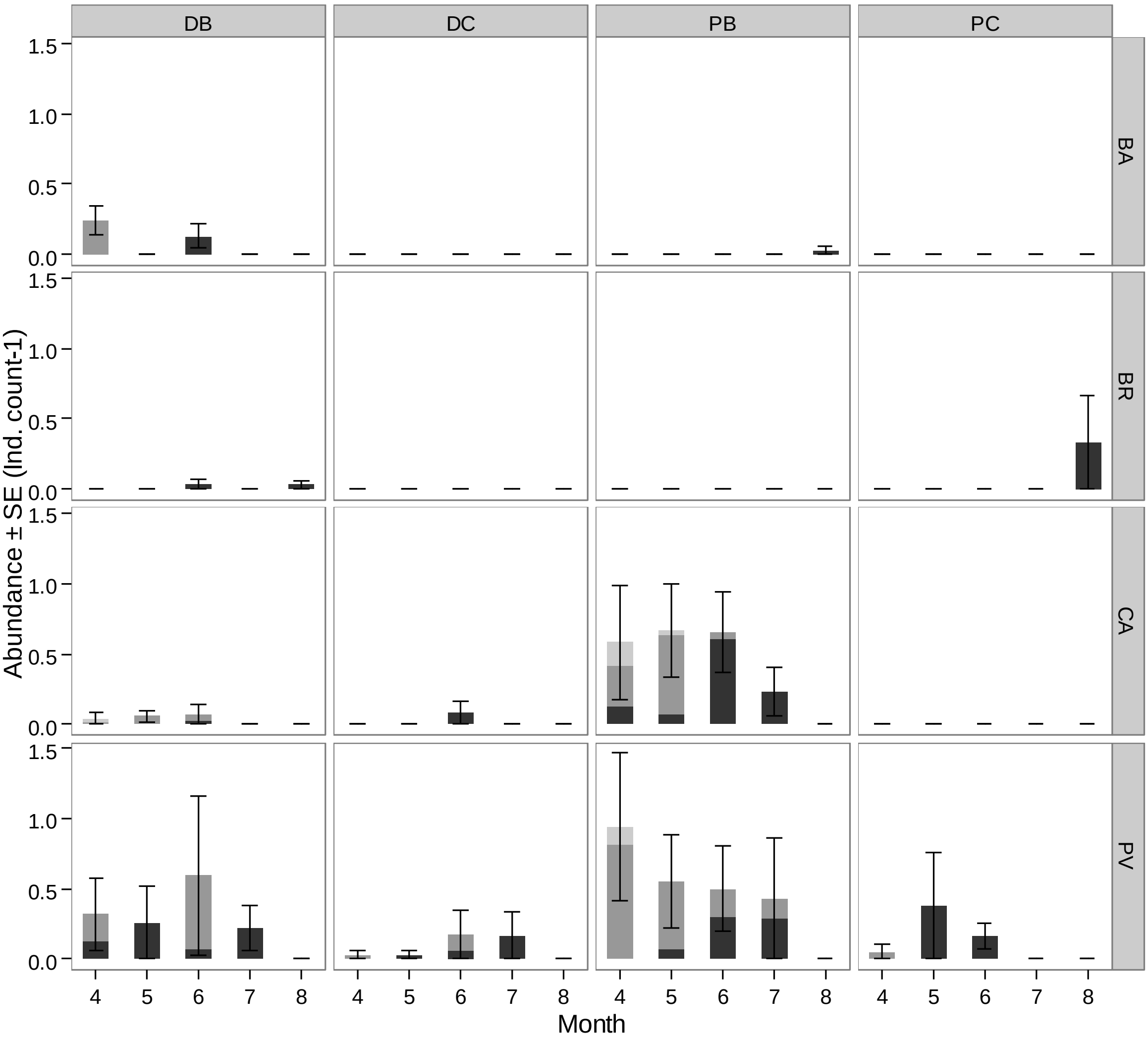


Supplementary material

Fig. S1: Mean abundances (ind. count^{-1}) of the juveniles of *D. annularis* (A) , *D. puntazzo* (B) , *D. sargus* (C) and *D. vulgaris* (D) observed per month, marina (Port-Vendres -PV-, Port-Barcarès -BA-, Cap d'Agde -CA- and Le Brusc -BR-) and habitat type (DB, DC, PB and PC). Results for Mèze are not represented since a total of only 3 individuals were observed in this marina. Colors correspond to the three development stages chosen in this study: post-settlement in light grey, intermediate in dark grey and pre-dispersal in black. Error-bars represent the standard error around the mean abundance found when all development stages were combined.

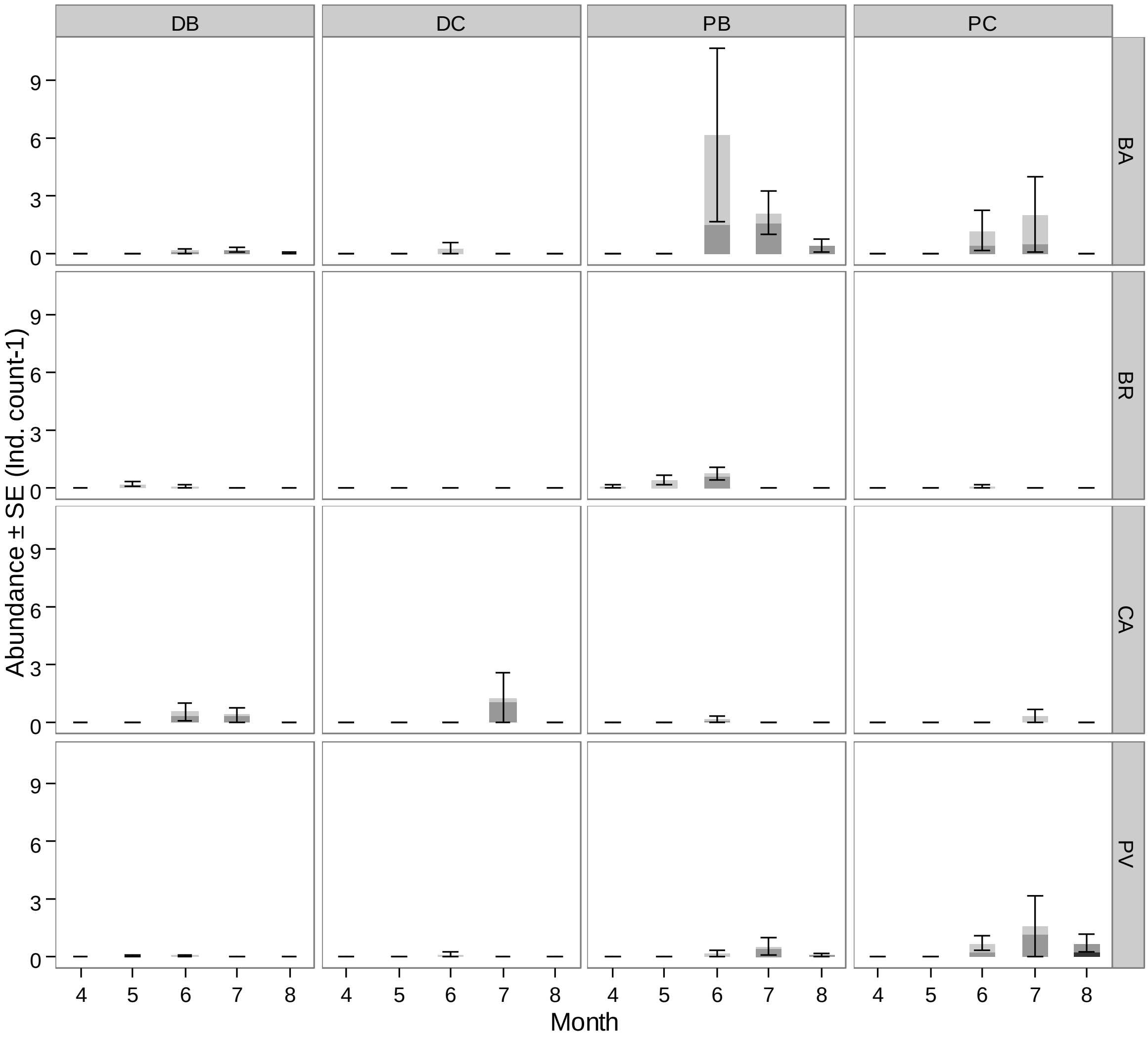


(A): *D. annularis*

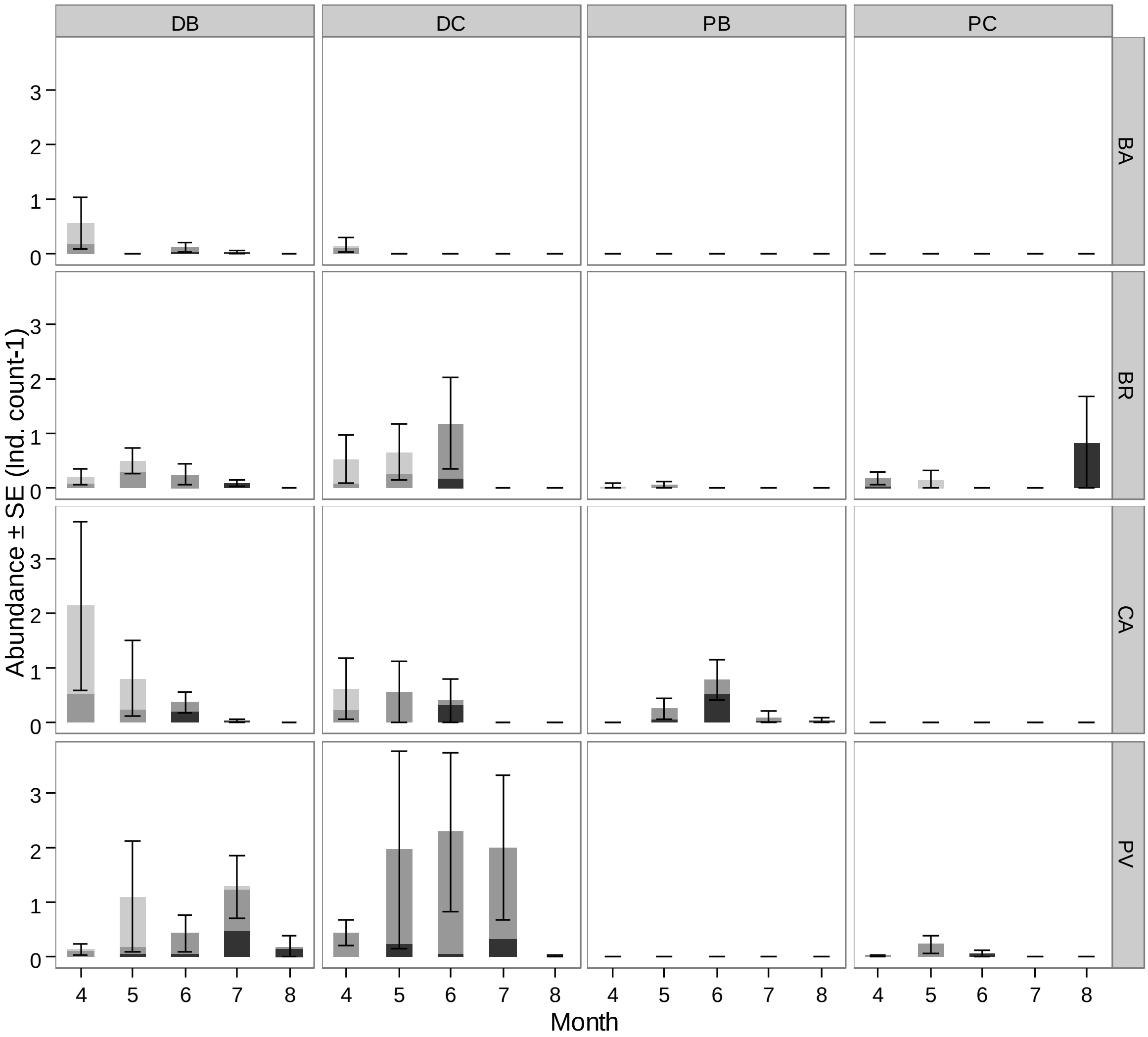


909

910 (B): *D. puntazzo*


DB
DC
PB
PC
BA
BR
CA
PV
Abundance ± SE (Ind. count-1)
0
3
6
9
4
5
6
7
8
Month

(C): *D. sargus*


DB
DC
PB
PC
BA
BR
CA
PV
Abundance ± SE (Ind. count-1)
0
1
2
3
4
5
6
7
8
Month

(D): *D. vulgaris*

Fig. S2: Evolution of monthly average temperatures in the five marinas studied during the sampling period (April-August).

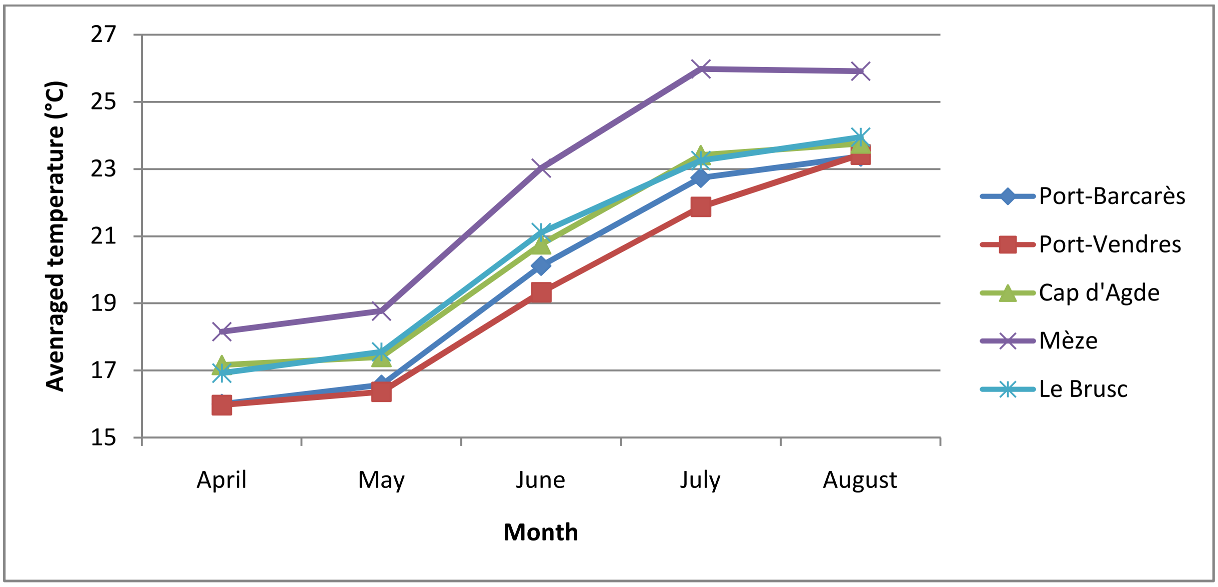


Table S1: Definition of development stages for the four species studied. (a) Data from Ventura et al. (2014). (b), (c) and (d) Data from Vigliola & Harmelin (2001). SL = standard length. TL = total length. Length used for development stages in Vigliola & Harmelin (2001) are given in SL. We estimated TL in our study. Relation between SL and TL are given in (Vigliola 1998): LT= a. LS with a = 1.257 for *D. puntazzo*. a = 1.290 for *D. sargus*. a = 1.283 for *D. vulgaris*.

Development stage	**SL (mm)**	**TL (mm)**
a) *D. annularis*		
Post-settlement		Settlement - 20
Intermediate		20 - 45
Pre-dispersal		>45
b) *D. puntazzo*		
Post-settlement	Settlement - 21	Settlement - 26
Intermediate	21 - 43	26 - 54
Pre-dispersal	> 43	> 54
c) *D. sargus*		
Post-settlement	Settlement - 23	Settlement - 30
Intermediate	23 - 49	30 - 63
Pre-dispersal	> 49	> 63
d) *D. vulgaris*		
Post-settlement	Settlement - 24	Settlement - 30
Intermediate	24 - 40	30 - 51
Pre-dispersal	> 40	> 51